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Increased allocation to reproduction reduces future competitive ability in a burying beetle

Running title: Reproductive allocation reduces competitive ability

Jon Richardson*, Josh Stephens & Per T. Smiseth

Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, U.K.

*Correspondence: J. Richardson, Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Charlotte Auerbach Road, Edinburgh, EH9 3FL, U.K.

E-mail address: jon.richardson@ed.ac.uk

Telephone: 0131 651 3612

Abstract

1. The existence of a trade-off between current and future reproduction is a fundamental prediction of life-history theory. Support for this prediction comes from brood size manipulations, showing that caring for enlarged broods often reduces the parent's future survival or fecundity. However, in many species, individuals must invest in competing for the resources required for future reproduction. Thus, a neglected aspect of this trade-off is that increased allocation to current reproduction may reduce an individual's future competitive ability.
2. We tested this prediction in the burying beetle, *Nicrophorus vespilloides*, a species where parents care for their offspring and where there is fierce competition for resources used for breeding.
3. We manipulated reproductive effort by providing females with either a small brood of 10 larvae or a large brood of 40 larvae and compared the ability of these females, and virgin females that had no prior access to a carcass, to compete for a second carcass against a virgin competitor.
4. We found that increased allocation to current reproduction reduced future competitive ability, as females that had cared for a small brood were more successful when competing for a second carcass against a virgin competitor than females that had cared for a large brood. In addition, the costs of reproduction were offset by the benefits of feeding from the carcass during an initial breeding attempt, as females that had cared for a small brood were better competitors than virgin females that had no prior access to a carcass, whilst females that had cared for a large brood were similar in competitive ability to virgin females.

5. Our results add to our understanding of the trade-off between current and future reproduction by showing that this trade-off can manifest through differences in future competitive ability and that direct benefits of reproduction can offset some of these costs.

Keywords: burying beetle; competition; cost of reproduction; life history trade-offs; reproductive allocation.

Introduction

The existence of a trade-off between current and future reproduction, also known as the cost of reproduction, is a central prediction of life history theory (Williams 1966). This trade-off is predicted because reproduction and somatic maintenance compete for the same pool of limited resources (Smith & Fretwell 1974; van Noordwijk & de Jong 1986; Lessels 1991; Roff 2002; Flatt & Heyland 2011), such that increased allocation to one function will reduce allocation to the other (Stearns 1992). Thus, individuals that allocate more to the production and care of current offspring should suffer from reduced future survival and/or fecundity. This prediction is supported by brood size manipulations used to experimentally alter current reproductive effort. Such studies show that parents rearing experimentally enlarged broods often suffer a future cost in terms of lower body condition (Lessels 1986; Reid 1987; Velando & Alonso-Alvarez 2003; Ratz & Smiseth 2018), impaired immunity (Hörak et al. 1998; Ardia 2005; Merino et al. 2006), higher predation risk (Veasey et al. 2000; Veasey et al. 2001; Kullberg 2002), increased parasite load (Richner et al. 1995; Oppliger et al. 1996; Lucas et al. 2005; Alt et al. 2015) or shorter lifespans (Jacobsen et al. 1995; Daan et al. 1996, Siefferman & Hill 2007). Alternatively, increased reproductive effort may be associated with the production of fewer or poorer-quality offspring in future reproductive attempts (Gustafsson & Sutherland 1988; Parejo & Danchin 2006; Oksanen et al. 2007). However, evidence for a cost of reproduction is mixed, as some studies find no relationship (or a positive one) between reproductive effort and future survival (Santos & Nakagawa 2012).

There are many potential explanations for why some studies fail to demonstrate the predicted trade-off between reproductive effort and future survival and/or fecundity, including variation in resource acquisition such that some individuals allocate greater amounts of resources to both current reproduction and future survival (van Noordwijk & de

Jong 1986), sex differences in parental effort (Santos & Nakagawa 2012), temporal and/or spatial fluctuations in resource availability (Reznick et al. 2000), or simply a lack of statistical power (Graves 1991). Furthermore, studies may fail to demonstrate this predicted trade-off if such costs are not recorded in the appropriate environmental context. For example, in many species, individuals must invest in their ability to compete for resources required for future breeding attempts. Thus, if increased reproductive effort reduces an individual's future competitive ability, we need to consider the trade-off between current and future reproduction in a context where there is competition for resources. Competitive ability is an important determinant of future reproductive success whenever individuals require access to scarce resources, such as food or nesting sites, in order to breed. Individuals may need to invest resources to maintain their competitive ability, in which case greater allocation to current reproduction may compromise an individual's future competitive ability. In support of this prediction, correlational evidence suggests that this cost is higher when population density (and presumably level of competition) is high (Festa-Bianchet et al. 1998; Oksanen et al. 2007). Great tits (*Parus major*) raising enlarged broods were less likely to claim high-quality nest-boxes (Fokkema et al. 2016), whilst male eastern bluebirds (*Sialia sialis*) raising reduced broods were better able to compete for nest cavities (Siefferman & Hill 2005a; Siefferman & Hill 2005b). However, other studies on great tits found no evidence that increased allocation to current reproduction reduced the ability to secure scarce nest-boxes (Fokkema et al. 2018) or winter roosting boxes (Fokkema et al. 2017). These conflicting results highlight the need for more studies on the trade-off between current reproduction and future competitive ability.

We address this gap by examining if increased investment to current reproduction reduces future competitive ability in the burying beetle *Nicrophorus vespilloides*. This

species breeds on the carcasses of small vertebrates that serve as food for both parents and offspring. Parents provide elaborate parental care, including brood defence, secretion of antimicrobials, and food provisioning to offspring (Eggert et al. 1998; Smiseth et al. 2003; Rozen et al. 2008; Arce et al. 2012). This species is well suited for studying whether increased allocation to current reproduction impairs future competitive ability. First, there is fierce intrasexual competition over carcasses, an ephemeral and high-value resource that is necessary for breeding (Safryn & Scott 2000). Second, there is some evidence for a trade-off between current and future reproduction in this species and the closely related *Nicrophorus orbicollis* as females caring for larger broods in the first breeding attempt suffer a reduction in lifespan (Creighton et al. 2009) and fecundity in future breeding attempts (Creighton et al. 2009; Ward et al. 2009; Billman et al. 2014). However, other studies find no evidence for a negative association between brood size and lifespan (Richardson & Smiseth 2019). Prior work suggests that resource competition is important to this trade-off. For example, inbred males that have low future reproductive potential are more willing to risk injury when competing for a carcass (Richardson & Smiseth 2017). Furthermore, females provide more care to their offspring when they experience competition prior to breeding, suggesting that competition provides cues about the likelihood of future reproductive opportunities (Pilakouta et al. 2016). However, it is currently unclear whether increased allocation to current reproduction would reduce future competitive ability.

Given that parents feed from an energy-rich carcass during breeding (Pilakouta et al. 2016), reproduction is associated with direct benefits (over and above those gained from the production of offspring). Thus, access to resources whilst breeding will mitigate some of the energetic costs of reproduction and may even increase future reproductive success by boosting the condition of breeding individuals relative to non-breeders. In support of this,

caring parents are often heavier at the end of reproduction (Creighton et al. 2009; Pilakouta et al. 2016; Gray et al. 2018; Richardson & Smiseth 2018; Richardson et al. 2019)

Furthermore, males that provide parental care are more attractive because access to carrion allows them to allocate more resources to sexual signalling (Chemnitz et al. 2017). Thus, studies on this species need to consider potential benefits gained from access to resources during breeding when testing for effects of increased reproductive effort on future competitive ability.

The aims of our study were threefold. First, we investigated whether increased reproductive effort reduced an individual's future competitive ability. To this end, we manipulated allocation to current reproduction by providing females with either a small brood of 10 larvae or a large brood of 40 larvae. We then recorded their success when competing for a new carcass against a virgin size-matched competitor. If increased current reproductive effort reduces future competitive ability, we predicted that females caring for a large brood would have lower competitive ability than females caring for a small brood. We also recorded female weight gain during the initial breeding attempt and the growth and survival of larvae in the experimental brood. Second, we investigated whether benefits of reproduction, such as access to resources during breeding, improved an individual's future competitive ability. Thus, we included a control treatment of virgin females, which had no prior access to breeding resources, and compared their competitive ability with females that had cared for a small or large brood. We predicted that females that had reared a brood of offspring would be more competitive than virgin females given that the former could boost their condition by feeding from the carcass during their initial breeding attempt. Third, there may be combined effects of increased reproductive effort and access to resources during breeding on an individual's future competitive ability. If so, we

predicted that females that had cared for a small brood would have higher competitive success than both virgin females of the control treatment and females that had cared for a large brood. This is because the former females would benefit from having had access to food unlike virgin females, whilst also investing less in their initial breeding attempt than females that had care for a large brood. We also recorded the lifespan of females to examine if the cost of increased reproductive effort had a similar effect on both future competitive ability and future survival. If the cost of reproduction negatively affects both competitive ability and survival, we predicted that females that had cared for a small brood would have a longer lifespan than virgin females and females that had cared for a large brood.

Methods

General methods

We used beetles from our outbred laboratory population maintained at the University of Edinburgh, UK. We used 3rd and 4th generation beetles descended from wild-caught beetles originally collected in Hermitage of Braid, Edinburgh, UK. All beetles were kept at 20°C under a 16:8 h light:dark cycle. Nonbreeding adults were housed individually in transparent plastic containers (12 cm x 8 cm x 2 cm) filled with moist soil and fed organic beef twice a week.

Experimental design

To investigate how allocation to current reproduction influenced future competitive ability, we first manipulated allocation to reproduction in an initial breeding attempt by providing females with either a small brood of 10 larvae or a large brood of 40 larvae. To this end, we

first paired females ($n = 67$) with an unrelated male from the stock population. To initiate breeding, we transferred each pair to a transparent plastic container (17 cm x 12 cm x 6 cm) lined with 1 cm of moist soil and provided them with a freshly thawed mouse carcass (Livefoods Direct Ltd, Sheffield, UK) of a standardised size (20–24 g; mean \pm SE = 22.01 ± 0.12 g). All beetles were outbred virgins and were bred within 3 weeks after sexual maturation to avoid variation in reproductive effort due to differences in age. We weighed each female prior to breeding, using this measure of pre-breeding mass to estimate mass change during breeding (see below).

We left pairs together with the carcass for 48 h to complete egg laying. Before the eggs hatched, we moved the female and the carcass to a new container with fresh, moist soil. At this time, we discarded the male because the presence or absence of the male has no effect on larval growth or survival under laboratory conditions (Bartlett 1988; Smiseth et al. 2005). When the eggs started hatching, we used the newly hatched larvae to generate small or large experimental broods, comprised of either 10 or 40 larvae, by pooling larvae from eggs laid by different females. We chose these brood sizes because they are within the natural range for this species (2 – 45 larvae; Smiseth & Moore 2002), and because they represent around half and double the average brood size (21 larvae; Smiseth & Moore 2002). Parents show temporal kin discrimination, and cannot distinguish between manipulated foster broods and their own broods as long as the larvae are at the same developmental stage (Oldekop et al. 2007). Given that parents kill any larvae that arrive on the carcass before their own eggs are expected to hatch (Müller & Eggert 1990), we only provided experimental females with a brood once their own eggs had hatched. Before placing the larvae on the carcass, we weighed the brood, which later allowed us to calculate offspring growth from hatching to dispersal (see below).

Females were left to rear their broods until the larvae dispersed from the carcass approximately 7 days later. When all larvae had dispersed from the carcass, we recorded the number of dispersing larvae and the total brood mass. We calculated average larval mass at dispersal in each brood by dividing the total brood mass by the number of larvae in the brood. At the time of dispersal, we also weighed each female to record her post-breeding mass. We then calculated mass change during breeding for each female by subtracting her pre-breeding mass from her post-breeding mass. Experimental females were then transferred to individual containers (12 cm x 8 cm x 2 cm) filled with moist soil and left undisturbed for 24 hours.

In the second part of our experiment, we tested for effects on the ability of females to compete for a future reproductive attempt. We did this by setting up contests for the possession of a fresh mouse carcass between a focal female and a size-matched, virgin competitor from the stock population. This design allowed us to use virgin female competitors as a reference point, such that we could determine whether any difference in competitive ability between females that had cared for a small or a large brood was due to an increase in competitive ability of the former and/or a reduction in competitive ability of the latter. Focal females included experimental females from the first part of our experiment that had cared for a small ($n = 34$) or a large ($n = 33$) initial brood, as well as virgin, control females that had not bred before ($n = 34$). We included these virgin, control females so that we could separate between any potential effects caused by the costs and benefits of reproduction on competitive ability. For all trials, the competitor was an unrelated, virgin female. All females were only used once in this experiment. Prior to the contests, we recorded body size of each female's by measuring the width of her pronotum using digital callipers (Müller et al. 1990). We size-matched our focal female and her

competitor by ensuring that they had a pronotum width within $\pm 6\%$ of each other (mean difference in pronotum width \pm SE = $0.08 \pm 0.12\%$; range: 0–5.66%; mean pronotum width for focal females \pm SE = 5.21 ± 0.018 mm; range = 4.52 – 5.91 mm; mean pronotum width for competitor females \pm SE = 5.21 ± 0.016 ; range = 4.65 – 5.77 mm). We did this to exclude any potential effects due to variation in body size given that body size is a major determinant of competitive ability in *Nicrophorus* beetles (Otronen 1988; Safryn & Scott 2000). We confirm that there was no difference in body size between focal females assigned to the three treatments (ANOVA: $F_{2,98} = 1.06$, $p = 0.34$; mean pronotum width for females that cared for a small brood \pm SE = 5.24 ± 0.029 mm; range = 5.14 – 5.77 mm; mean pronotum width for females that cared for a large brood \pm SE = 5.19 ± 0.022 mm; range = 5.14 – 5.91 mm; mean pronotum width for virgin, control females \pm SE = 5.19 ± 0.022 mm; range = 4.52 – 5.74 mm). We ensured that focal females and their competitors were the same age to exclude any potential effects due to age-related differences in competitive ability (Trumbo 2012). To distinguish between the focal female and her competitor, we marked each female by applying either one or two small spots of correction fluid to their elytra. Such marks are short lasting, nontoxic and have no discernible effect on behaviour (Hagler & Jackson 2001; Richardson & Smiseth 2017; Georgiou Shippi et al. 2018). We alternated which of the two females (i.e. the focal female or her competitor) was given two spots between experimental trials to exclude any potential effect of marking on the outcome.

To initiate contests, we transferred the focal female and her competitor to transparent plastic containers (17 cm x 12 cm x 6 cm) with 1 cm of moist soil and a freshly thawed mouse carcass of a standardised size (20–24 g; mean \pm SE = 22.15 ± 0.12 g). We then left the pair undisturbed for 3 days, after which we determined the outcome of the contest.

We identified the winner as the female that was present on or near the carcass after 3 days, and the loser as the female that was away from the carcass (Safryn & Scott 2000; Trumbo 2012). Prior work suggests that 3 days is sufficient time for competing beetles to settle the dispute over ownership of the carcass (Trumbo 2007; Pilakouta et al. 2016; Richardson & Smiseth 2017). In the majority of cases ($n = 92$), it was straightforward to identify the winner as one female was present on the carcass whilst the other female was away from the carcass. However, in a few cases ($n = 9$), the outcome was ambiguous because neither female was present on the carcass. We excluded these trials from our further analyses. This gave the following final sample sizes of our experiment: females that had cared for a small brood ($n = 32$); females that had cared for a large brood ($n = 30$) and virgin, control females that had not bred prior to the contest ($n = 30$). After the contest, we transferred the focal female to an individual transparent plastic container (11 cm x 11 cm x 3 cm) filled with moist soil and maintained her following the protocol for beetles in the stock population (see above) and checked her twice weekly until death to record lifespan.

Statistical analysis

We used R version 3.6.0 (R Core Team 2019) for all analyses. For females that had cared for a brood of offspring, we used general linear models fitted with normal error structures to examine whether brood size (10 or 40 larvae) influenced female mass change during this initial breeding attempt, the average size of offspring at dispersal, average offspring growth from hatching to dispersal or the proportion of the brood surviving to dispersal. Data on the outcome of contests (win or loss) were analysed using binary logistic regression. This model included treatment of the focal female (female that had cared for a small brood, female that had cared for a large brood, or virgin, control females that had not bred before), the relative

difference in body size between the focal female and her competitor, and the size of the carcass that the females competed over as fixed effects. Finally, data on lifespan was analysed using Cox's proportional hazards. This model included the treatment of the focal female and the outcome of the trial (win or loss) as fixed effects.

Results

Does increased allocation to reproduction reduce female weight change or offspring performance?

Increasing reproductive allocation experimentally had a negative effect on female mass change as females that cared for a small brood of 10 larvae gained more mass during breeding than females that cared for a large brood of 40 larvae (estimate \pm SE = 0.024 ± 0.0069 g, $t = 3.49$, $p = 0.00087$; Figure 1). This represents a 13% increase in body mass for females that had cared for a small brood (mean pre-breeding mass \pm SE = 0.2635 ± 0.0069 g) versus a 5% increase in mass for females that had cared for a large brood (mean pre-breeding mass \pm SE = 0.2721 ± 0.0072 g). However, our brood size manipulation had no effect on offspring performance as there was no difference in the average mass of larvae at dispersal (estimate \pm SE = 0.035 ± 0.022 g, $t = 1.57$, $p = 0.12$), the average growth of larvae from hatching to dispersal (estimate \pm SE = 0.043 ± 0.022 g, $t = 1.94$, $p = 0.056$) or larval survival (estimate \pm SE 0.032 ± 0.045 , $t = 0.73$, $p = 0.46$) between females caring for small or large broods.

Does increased allocation to reproduction reduce future competitive ability?

As predicted, increased allocation to current reproduction in an initial breeding attempt reduced future competitive ability as females that had cared for a small brood were more likely to win a subsequent contest against a size-matched virgin competitor than females that had cared for a large brood (estimate \pm SE = 1.84 ± 0.57 , $z = 3.23$, $p = 0.0036$; Figure 2) or a virgin, control female that had not bred before (estimate \pm SE = 1.30 ± 0.56 , $z = 2.32$, $p = 0.041$; Figure 2). However, there was no difference between females that had cared for a large brood and virgin, control females (estimate \pm SE = -0.54 ± 0.54 , $z = -0.99$, $p = 0.32$; Figure 2). The outcome of the contest was not influenced by the relative size-difference between the focal female and her competitor (estimate \pm SE = 27.02 ± 20.88 , $z = 1.29$, $p = 0.19$) or the size of the carcass over which the females competed (estimate \pm SE = -0.15 ± 0.21 , $z = 1.29$, $p = 0.19$).

Does increased allocation to reproduction reduce lifespan?

Increased allocation to reproduction did not influence future survival as there was no difference in lifespan between females that had cared a small and females that had cared for a large brood (Hazard ratio \pm 95 % CI = $0.894 [0.537, 1.486]$, $z = -0.43$, $p = 0.66$). Similarly, there was no difference in lifespan between virgin, control females and females that cared for a small brood (Hazard ratio \pm 95 % CI = $0.800 [0.476, 1.344]$, $z = -0.84$, $p = 0.40$) or females that cared for a large brood (Hazard ratio \pm 95 % CI = $0.715 [0.424, 1.203]$, $z = -1.26$, $p = 0.21$). In addition, the outcome of the contest did not influence female lifespan as winners lived a similar number of days as losers (Hazard ratio \pm 95 % CI = $0.770 [0.503, 1.180]$, $z = -1.21$, $p = 0.23$).

Discussion

Here we show that increased allocation to current reproduction due to brood size manipulation incurred a cost of reproduction in terms of reduced future competitive ability in the burying beetle *Nicrophorus vespilloides*. In support of this, females that had cared for a large brood of 40 larvae were less likely to win a future contest against a size-matched, virgin competitor than females that had cared for a small brood of 10 larvae. We also show that females benefitted from breeding by gaining mass by feeding from the carcass acquired for reproduction. We then show that this benefit can offset some of the costs of reproduction by improving the future competitive ability of breeding females relative to virgin females that had no prior access to a carcass. Females that had cared for a small brood, and who had gained the most mass during breeding, were more likely to win a future contest against a size-matched, virgin competitor than were virgin females. In contrast, females that had cared for a large brood, and who had gained the least mass during breeding, were as likely to win a future contest as virgin females. Thus, the benefit of feeding from the carcass in an initial breeding attempt was cancelled out by the increased costs of reproduction when females cared for a large brood. Finally, we found no evidence that increased allocation to current reproduction came at a cost in terms of reduced future survival when females competed for a carcass required for future breeding opportunities. Below we provide a more detailed discussion of our results and their wider implications for our understanding of the cost of reproduction and life-history trade-offs.

We found that females that had cared for a large brood were less successful in a subsequent contest against a size-matched, virgin competitor than females that had cared for a small brood. Thus, our study provides evidence that the increased allocation to reproduction due to brood size enlargement came at the cost of reduced future competitive ability in *N. vespilloides*. Given that burying beetles require access to a carcass – a rare and

ephemeral resource – in order to reproduce (Scott 1998), our results demonstrate that allocation to current reproduction impairs future reproduction through its detrimental effect on future competitive ability. Our results are in keeping with prior work on cavity nesting birds demonstrating that brood size manipulations affect success in subsequent contests for nest boxes required for reproduction (Siefferman & Hill 2005a; Siefferman & Hill 2005b; Fokkema et al. 2016). A likely explanation for our finding is that females that had cared for a large brood expended more energy during parental care than females that cared for a small brood, impairing their ability to invest resources in future competitive ability. Our finding that allocation to reproduction reduces competitive ability highlights that it is important to consider the context in which the cost of reproduction is measured when studying life history trade-offs. For example, experimental studies may underestimate the cost of reproduction if the cost is measured in a context with limited scope for competition. Similarly, in studies conducted in the wild, there may be variation in the intensity of competition between different species, populations or years, and such variation may be important in determining the cost of reproduction. Thus, we encourage future work to consider the contexts under which a cost of reproduction is measured. For example, future work may examine whether the cost of reproduction is greater when measured when there is greater scope for competition than when studied in a context where there is limited scope for competition.

We found that females that had cared for a small brood were better competitors than virgin, control females, whilst there was no difference between females that had reared a large brood and virgin females with respect to their competitive ability. Thus, our results suggest that females that had cared for a small brood gained an increase in competitive ability compared to virgin females, whilst there was no reduction in the

competitive ability of females that had cared for a large brood. Our results derive from a design where we compared the competitive ability of females that had cared for a small or large brood with that of virgin, control females. Thus, when interpreting our results, it is important to consider potential differences between virgin females and females that had cared for a brood, and how such differences could account for our results. For example, females that had cared for a brood may have gained experience in fighting that would improve their future competitive ability, and such females may also be in different condition from virgin females because they have been exposed to the costs and/or benefits of reproduction. We can discount any effects due to experience in fighting given that females that had cared for a brood did not compete for the carcass during their first breeding attempt in our experiment. It also seems unlikely that incurring the costs of reproduction would make females *better* competitors as allocation of resources to egg laying and parental care should decrease their condition and thereby their future competitive ability. Instead, the most likely explanation for the increase in competitive ability of females that had cared for a small brood relative to virgin females is that the former benefitted by feeding from the energy-rich carcass during breeding. In support of this, we found that females that had cared for a brood gained mass during their initial breeding attempt. Furthermore, females that had cared for a small brood gained more mass during their initial breeding attempt than females that had cared for a large brood. Thus, taken together, our results suggest that females that had cared for a brood benefit by feeding from the carcass, thereby boosting their own condition and increasing their competitive ability, but that this benefit was offset by the greater energetic costs of caring for a large brood. In other words, females that had cared for a small brood gain a net benefit from having access to food from the carcass

during breeding, but this benefit is cancelled out by the cost of increased allocation to reproduction in females that had cared for a large brood.

Burying beetles in the genus *Nicrophorus* are capital breeders that acquire resources prior to breeding in the form of a small vertebrate carcass. The carcass serves as a source of food for parents as well as offspring, meaning that parents can boost their own condition by feeding from the carcass during breeding. Indeed, prior work shows that mass gained during the breeding attempt can be used as a proxy for allocation to future reproduction (Creighton et al. 2009; Billman et al. 2014). Taken together, our results provide evidence for combined effects of the cost of increased allocation to reproduction and the benefit gained from access to resources on the cost of reproduction in our system. In the case of females caring for enlarged broods, these effects cancel out such that females caring for a brood of 40 offspring have a competitive success equivalent to that of a virgin female with no prior access to resources. Furthermore, our results highlight the importance of considering direct benefits gained from reproduction (over and above those gained from the production of offspring). In our system, as in some other capital breeders, such as necrophagous or parasitoid insects, these benefits are gained by feeding from the resource acquired for reproduction (Rivero & West 2005; Pilakouta et al. 2016). However, similar effects may occur in other species – regardless of whether they are capital or income breeders – if, for example, breeding provides experience that reduces the cost of parental care in subsequent breeding attempts (e.g. Cichoń 2003; Barbraud & Weimerskirch 2005; Daunt et al. 2007). We encourage future work to examine the effects of direct benefits of reproduction on the cost of reproduction and life history trade-offs in both capital and income breeders by including appropriate control treatments in experimental designs.

There was no difference between females that cared for a small or a large brood in the average size of larvae at dispersal or the proportion of offspring in the brood that survived to dispersal. Thus, we found no evidence that experimentally increasing a parent's allocation to reproduction resulted in detectable costs to the offspring's performance. Potentially, parents caring for an enlarged brood could respond by shifting some or all of the costs to their offspring, producing fewer or poorer quality offspring as reported in some bird species (Mauck & Grubb 1995; Velando 2002). Alternatively, such parents could respond by allocating more to the current breeding attempt, resulting in a subsequent decline in future reproduction by reducing future survival, fecundity or competitive ability, as reported in other bird species (Jacobsen et al. 1995; Daan et al. 1996, Siefferman & Hill 2007). Taken together, our results show that *N. vespilloides* females caring for larger broods respond by reducing their allocation to future competitive ability rather than by shifting the costs to their offspring (i.e. by investing fewer resources into each offspring).

Life-history theory predicts that increased investment to current reproduction should come at the cost of future reproduction because an increase in the amount of resources invested to the current breeding attempt means fewer resources available for investment to somatic maintenance and future breeding attempts. However, empirical evidence for a cost of reproduction is mixed (see Santos & Nakagawa 2012). Typically, the cost of reproduction has been studied by examining effects on future survival (i.e. the probability of surviving to breed again) or future reproductive success (i.e. the likelihood of producing a second brood or the number and quality of offspring produced in future breeding attempts). Here we demonstrate that an additional way that increased allocation to reproduction comes at a cost to future reproduction is through an effect on future competitive ability. Whilst we focused on intraspecific competition for a resource required

for breeding, we argue that similar effects may occur in other social contexts. For example, the cost of reproduction may also depend on the extent and intensity of sperm competition or competition for mating opportunities. Understanding the different environments and social contexts in which we can detect a trade-off between current and future reproduction may help to resolve the mixed empirical evidence for the cost of reproduction.

In conclusion, our study advances our understanding of life history theory by demonstrating that the costs of increased allocation to current reproduction can manifest through differences in competitive ability. By examining the effect of brood size manipulation in the context of resource competition we can reveal evidence for a trade-off between current and future reproduction that would be missed if we had only considered traditional proxies of investment to future reproduction such as survival or fecundity. In fact, we found no evidence for a negative effect of allocation to reproduction on lifespan in our study. This result could be erroneously interpreted as a lack of evidence for a trade-off between current and future reproduction in our system if we did not consider additional ways that parents may pay a cost of reproduction within the context of competition for breeding resources.

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Author contributions

JR conceived the study, designed the experiment, analysed the data and led the writing of the manuscript. JS collected the data. PTS contributed to experimental design and writing of the manuscript. All authors read and approved the final manuscript.

Data availability

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h18931zh5> (Richardson et al. 2020).

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Figure legends

Figure 1 – Mean mass change during breeding (g) \pm SE for females that cared for a small brood of 10 offspring or a large brood of 40 offspring.

Figure 2 – Percentage of trials won (black bars) or lost (grey bars) by control virgin females that had no prior access to a carcass, females that had cared for a small brood of 10 offspring in an initial breeding attempt and females that had cared for a large brood of 40 offspring in an initial breeding attempt when competing for a new carcass against a size-matched virgin female competitor. Number of trials for each treatment were; control females (n = 30), females that had cared for a small brood (n = 32) and females that had cared for a large brood (n = 30).



